Nest Site Selection and Egg Laying Behaviour in Seabirds

GCAS 2006/07: Personal Research Project
Alison McKellar: 57194538
Due Date: Fri 16th February 2006

TABLE OF CONTENTS **Page Number**

INTRODCUTION

Seabirds are described as birds that rely on the marine environment for food resources, they spend a substantial part of their lives foraging in the marine environment. Foraging is generally done alone and they feed on krill, squid and fish.

Seabirds make up 3% of the worlds bird species. There are 328 species of seabirds in four orders. Spenisciformes is the penguins and there is 17 species in one family. Procellariiformes is the albatrosses, shearwaters, petrels, diving petrels, and storm petrels and there are 125 species in four families. Pelecaniformes is the pelicans, tropicbirds, frigatebirds, gannets and cormorants and there are 61 species in five families. Charadriiformes is the gulls, terns, skuas, skimmers and auks, and there are 128 species in four families.

Seabirds live longer and breed later than the other bird types. Some albatross and petrel species live for more than 60 years. Mortality rates are low in adults and offspring.

Many seabird species are threatened by human activities. This is mostly as seabird by-catch through commercial and private fishing. Many of these species are at risk of extinction, particularly the albatross, petrels and shearwaters. They are attracted to the bait used by boats and get caught in the fishing hooks and lines. They are then dragged down into the ocean where they drown. Seabird breeding sites are all threatened by human activities. They are lost through increased human settlement and through human degradation such as oil spills. Humans have introduced invasive animals such as rats to offshore islands which predate on seabirds while they are on land breeding.

Seabirds are found widely throughout the world's oceans, both in the Northern and Southern Hemisphere. They are found up in the Arctic and down in the Antarctic. Seabirds are known for often undertaking long annual migrations.

Most seabirds breed once a year, every year, and raise one brood a year. Larger species such as the albatross breed every two years due to the high energy requirements and the long time it takes to raise a chick, for example the grey-headed albatross. Seabird species are generally monogamous and both parents help with raising the chick. Breeding generally begins at three years of age in seabirds. Clutch size is generally between one and three eggs in size. Breeding in seabirds usually occurs in the summer.

This review will look at two sections of seabird breeding biology. These are, nest site selection and egg laying behaviour. Under nest site selection, the general global distribution of breeding seabirds, breeding habits, choosing sites, range of sites, nest types, nest material and building, and nest site fidelity will be examined and discussed. Under egg laying behaviour, general egg laying patterns, size difference between eggs, clutch size, factors that influence egg development and laying, egg size in relation to female body size, and egg composition will be examined and discussed. This review will be written on general traits, and will point out examples of unexpected behaviour and traits. The review will look at life history traits from an evolutionary aspect.

Sections of this review may be used by Dr Melanie Massaro as part of a chapter on general seabird breeding biology to be published on UNESCO (United Nations Education, Scientific and Cultural Organtisation) website, www.unesco.org. The other sections written by other scientists for this general seabird breeding biology chapter are: incubation, mate choice, mate fidelity and chick raising.

NEST SITE SELECTION

- General global distribution of breeding seabirds

Seabirds breed at higher latitudes and in colder environments than any other vertebrate (Hamer 2002). Seabirds are found in all oceans of the world and in both hemispheres. Areas of upwelling in the oceans are important places for seabirds to feed as fish, krill and squid are brought to the surface. Seabird numbers are higher in polar regions than tropic regions.

Seabirds are found nesting mostly on remote islands or headlands, this is so they are away from mammalian predators and are in site of the sea where their food resources are found (Warham 1990). Birds tend to nest close to their food resources, an exception is the Snow petrel which breeds on the mainland of Antarctica, this is 300km from the coast and any food resources (Lofgren 1984). An interesting example of an unexpected breeding site is the Mottled petrel, a small population of this species lives on an island in the middle of a freshwater lake (Warham 1990). Areas that provide easy take-off and landing are also important when selecting breeding sites (Warham 1990).

Most birds arrive at their breeding sites over a short period of time. It is generally the males who arrive at the breeding sites first and may compete with each other for the most sought after nest sites. This does not occur in Emperor penguins, it is the females that generally return before the males (Bried 2002). Many seabirds return to the breeding site months before the breeding season begins, this is to defend the best nest sites (Furness 1987).

Temperature, food availability, age, experience and length of daylight hours are all factors that affect the timing of seabird breeding cycles (Hamer 2002). Food location is

particularly important in the timing of breeding in seabirds (Hamer 2002), it is often spread in patches through the ocean so its location in relation to suitable breeding sites is important. In order for seabirds to have a successful breeding season, the available food resources must be able to support both parents and the offspring.

Breeding habitat selection involves two choices, the first is the location of the colony site, and the second is the location of the nest site. In colonially breeding birds this choice is very distinct, in solitary breeders the two choices are functionally the same (Hamer 2002).

- Breeding habits

The general trend for seabird species is that they nest colonially (Clode 1993). Ninety six percent of seabird species are colonial nesters, this is higher than any other bird type (Coulson 2002). Lek and polygamy mating systems are absent in seabirds (Coulson 2002). There are a few species that are both colonial and solitary breeders. Common Terns in Europe are mostly colonial, but there are some pairs that breed in isolation from other pairs (Cramp 1985). All penguin species are to some degree colonial (Davis 2003). Colonies are often found in areas absent of mammalian predators and with few avian predators (Coulson 2002).

Colonial breeding has evolved on more than one occasion during the evolutionary history of seabirds. This is evident as all of the major orders of seabirds have some colonial species. Selection pressures to breed colonially would have occurred at different times, resulting in the convergent evolution of colonial breeding (Coulson 2002).

Colonies can vary in size from a few pairs in the Royal Albatross colony at Taiaroa Head, New Zealand, to millions of pairs in the Sooty Tern colony on Christmas Island (King 1983).

(Cramp 1985) suggested four possible reasons explaining why seabirds breed in colonies.

1. Shortage of nesting sites. The birds are restricted in space to create nests so they crowd together on the best sites.
2. Defense against predation. By sticking together in large groups, the birds have more eyes to watch and warn when predators are near. An individual's chance of being a predators target also decreases when colony size increases. The birds all breed at the same time, so predators are swamped with prey choices so an individual chick's chance of surviving increases.
3. A colony is a safe place. Colonies provide protection for birds, and this is an important factor when selecting nest sites.
4. The colony is used as information centre. Birds use colonies to identify food source locations and can learn from successful breeders.

Nesting in a colony brings many advantages to the seabirds. These include: protection from predators, ability to detect predators sooner and the less experienced breeders can learn from more experience birds in the colony (King 1983). When resources, such as nest sites are limited, seabirds will need to form colonies and nest close together in order to have a successful breeding season. Colonially breeding birds can cooperate in feeding when food supplies are clumped (Clode 1993). Colonies also make it easier to find a replacement mate if a bird looses their mate (Nelson 1980). Colonies increase social interaction between the birds in the colony (Coulson 2002).

The disadvantages of colonial living include, predators are more attracted to the colony as they are more conspicuous and provide more prey (King 1983). Competition for resources such as food, mates and shelter increase when birds nest in colonies. The risk of the transfer of parasites and microbes are increased because the birds are in close contact with each other. When site fidelity occurs, parasites build up in the nest sites and increase each year (Coulson 2002). As the animals are living close to each other, intraspecific aggression increases. Although fighting is often rare in colonially breeding seabirds, tension between the birds is increased (Coulson 2002). Colonial breeding in seabirds presents many disadvantages to the birds, but it is evident that the advantages outweigh the disadvantages as 96% of seabird species live in colonies.

Colony size is related to the feeding range of the species. Species with larger feeding ranges will have larger colonies (Coulson 2002). Size and global position are not selection pressures in breeding type choice, colonial species are represented across all latitudes where seabirds are found and are represented all throughout the size range of seabirds (Coulson 2002). Colonial breeding is found in both nocturnal and diurnal species (Coulson 2002). Colonial breeding restricts where and when birds can breed (Coulson 2002), there must be enough space and food resources to support all the birds and their chicks. When nesting sites are in shortage, competition for nesting sites will increase between the species wanting to nest there (Hamer 2002). For example, on King George Island in Antarctica, Chinstrap penguins compete with Adelie penguins for nesting sites and displace the Adelie penguins, this results in lower reproductive success (Hamer 2002). Colonial breeding makes movement into new areas and the formation of new colonies difficult (Coulson 2002).

- Choosing Sites

Seabirds are bound to land as their eggs must be kept warm while they are incubated and hatch (Davis 2003), because of this all seabird breeding occurs on land. Many seabirds exhaust their body reserves during breeding as they are must stay on the land and many do not feed for a few months (Bried 2002).

Many factors influence the site a seabird will choose to nest. These can be abiotic or biotic factors. They include: food, competition for sites from other birds, predation, parasitism, social factors, weather and human disturbance (King 1983). Food supply is the most significant factor in nest site selection. Most birds will select a nest site that is close to the coast, where the food supply is. The best food supplies support the greatest concentration of seabird nests (King 1983). An exception to this is Grey Gulls which nest in the Peruvian Desert, which is a long way from water and therefore food resources. Sea cliffs are often chosen as they are relatively free of mammalian predators. The cliffs also provide easy escape from any potential predators. Protection from predators is very important because if the birds need to leave their nests to forage for food, the nests are often left unattended (Bried 2002). The weather can be a limiting factor in nest site choice. Areas of high flooding and storms can restrict nest sites. In Arctic and Antarctic regions, seabirds choose sites that are free of ice and snow. This can restrict sites available for breeding and nesting (King 1983). The birds also need to protect themselves from the weather, as this saves energy and prevents eggs and chicks becoming too cold in polar environments, and over heating in the tropics (Hamer 2002). This is done by nesting in burrows and in the shade of trees. Human interference can be a positive impact in nest site selection. For example least terns and herring gulls nest on human structures

such as roof tops. Humans can also have a negative impact on seabird breeding, in areas that have been disturbed by human interference nests and colonies are sometime abandoned (King 1983). Many species are able to change their breeding habitat if any of the above conditions change (Hamer 2002). Types of foraging habitat, daily flight distances and energetic considerations are all factors of the birds foraging behaviour that impact breeding habitat choice (Hamer 2002). Nest sites are often chosen for easy access in and out of the nest (Bried 2002).

Within the colony, it is the nest sites at the periphery of colonies that are generally less productive than those in the centre (Bried 2002). The centre sites are often taken by the older, more experience breeders who generally arrive at the colonies first.

- Ranges of sites

Nest sites range from steep cliff edges to flat ground. Seabirds lay eggs in burrows, crevices, trees, bushes and in the open. Some seabird species build no nest, they lay their eggs on bare rock (Dunnet 1990). This includes most skua, albatross and gull species. Seabirds nest on the mainland, in marshes, on the coast, on oceanic islands and sometimes in roofs (Hamer 2002). It is common to find many different sea bird species nesting on all of the nest site habitats down the same cliff. If spatial heterogeneity is high in an area then more species can breed in that area as niche diversification is higher (Hamer 2002).

(Lack 1966) divided seabirds into three groups based on their living habits.

1. Pelagic or offshore feeders – the Auks, Shearwaters and Petrels. These birds nest in large dense colonies on sea cliffs and rocks that are relatively inaccessible. They lay a single white egg and the young hatch under-developed.
2. Inshore feeders – the Gulls and Terns. These birds breed in small colonies along coasts, islands and headlands. They lay a small clutch of camouflaged eggs. The young are feathered, have open eyes and are able to run when they hatch.
3. Solitary nesters – the Marine Waders. These birds feed near the nest and lay 3 or 4 camouflaged eggs. The young are under-developed when they hatch.

Most seabirds nest on cliffs of small islands, the cliffs offer many types of nesting sites (Nelson 1980). In one cliff site many birds can be found nesting on it. Gannets nest on the broad flat edges, shags nest in the lower 10-20m on broad ledges and low stepped flat topped stacks, razorbills nest in the cracks, small ledges and projections, fulmars nest on steep slopes, and terns nest on the flat ground (Nelson 1980). Over the nesting habitats of a cliff edge, it is often the fulmars and gannets that are most dominant in the competition for nest sites, gannets have been known to toss guillemots over the cliff edge (Nelson 1980). Cliffs provide great wind and air space properties for birds, which makes take-off and landing easier (Nelson 1980). In Antarctica and the Arctic, there is few suitable cliff sites so birds nest on flat ground, burrows or on the ice (Nelson 1980). Chinstrap penguins nest on easy cliffs, they pull themselves up with their bills and toenails (Nelson 1980).

- Nest Types

Nest site type ranges within the seabird orders and sometimes within the species (Hamer 2002). For example, Red- footed boobies nest in trees and on the ground (Schreiber 1996). Little penguins are the most heterogeneous penguin species in terms of breeding sites. They nest in burrows, under rocks and bushes, as solitary pairs or as loose aggregations (Davis 2003). There are few seabirds that are restricted to one nest site type, and seabirds have utilized most niches on islands (Nelson 1980) (Table 1). Species with rapid population growth tend to show higher habitat selection variation (Furness 1987). For example, Herring Gulls are a species with rapid expansion, they occupy coastal cliffs, rocky outcrops, grassy slopes, boulders, rocky beaches, sand dunes, shingle and moorlands (Furness 1987).

Seabirds often build surface nests when they are too big to burrow, for example the Royal and Wandering albatross nests are shallow depressions on the surface where the bird sits (Warham 1990). Penguins, skuas and gulls are mostly surface nesters (Lofgren 1984). Surface nests are often situated in areas that protect the birds from the weather, such as wind. Rocks, trees and tussocks can provide this shelter. 20% of the petrel species are surface nesters (Warham 1990). Ground nesting is common in areas where ground predators are absent, for example on oceanic islands (Lofgren 1984). Sometimes with surface nesters, the nests are so densely spaced at the colony that there is only just enough room for take-off and landing between the nests (Lofgren 1984).

Crevice nests protect the birds from the harsh climate and predators. They occur as crevices on cliff faces, under rocks, and in caves (Warham 1990). They are used mostly

by small birds, such as the storm petrel. 4% of petrel species are crevice nesters (Warham 1990).

Burrowing to nest provides many advantages for seabirds. It provides protection from cold and hot weather conditions, it hides the birds and eggs away from predators, the egg can be left alone while the adult gets food, and many burrows can be situated in areas where space is limited (Warham 1990). Digging a burrow is very energy expensive, but a positive aspect is that it can be used for many years (Warham 1990). Burrows are often dug because birds are vulnerable on land and so they nest in burrows to protect themselves (Nelson 1980). Burrow nesters use olfactory cues to locate their own burrow amongst the other burrows (Nelson 1980). Competition for burrows does occur, storm petrels on the Galapagos Islands have 77% nest failure because of competition (Nelson 1980). Two different species may use the same burrow in different breeding seasons in one year, for example, Little Shearwater and White faced storm petrels on the Giant Salvage share burrows (Nelson 1980). Many burrows can occur in a small area, mutton birds on Green Island in the Bass Straits crowd nine burrow entrances into one square meter (Nelson 1980).When density is great in a colony, burrowing can increase the number of nest sites an area can support (Warham 1990). Burrows are easier nests to defend than open nests (Furness 1987), but the birds inside them are vulnerable to ground predators such as snakes, rats and cats (Furness 1987).

Nests in trees provide easy landing and take-off for the birds. They are protected from ground predators and in warm climates such as the tropics, the birds can avoid the hot ground (Lofgren 1984). The White Tern is an example of a seabird that nest in trees, it nests directly on the branches (Lofgren 1984). The red-footed booby is a fully arboreal

species, this is really unexpected in seabirds (Nelson 1980). Some seabird species nest in holes in trees, it is very rare but does occur. The Golden Bosunbirds on Christmas Island nest in tree holes, it is expected to have evolved to avoid competition for other nest site types (Nelson 1980).

Some seabird species build no nest at all. The Fairy Tern nests on bare shingle (Nelson 1980). Emperor penguins incubate their eggs in their feet (Bried 2002).

Table 1: Nesting Sites Used by Seabirds Source:(Bried 2002)

Seabird Type	Burrows	Crevices	Boulders or Rock Cavities	Tree Holes	Cliffs, Ledges	Trees	Flat Ground or Smooth Slopes	Steep Slopes	No Nesting Site
Sphenisciformes	†		†				†	†	†
Procellariiformes	†	†	†		†		†	†	
Pelecaniformes									
Tropicbirds		†	†	†	†		†		
Sulids					†	†	†		
Frigatebirds						†	†		
Cormorants					†	†	†	†	
Charadriiformes									
Skuas and jaeger							†		
Gulls and terns					†	†	†		
Alcids	†			†	†				

- Nest Building and Nest Material

Nests are generally made from material that is nearby and readily accessible to the birds. When they nest in high densities, nest structure may change (Warham 1990), possibly due to increased competition for sites and materials. Nest building involves collecting and delivering the material, and building the nest.

Once the nest has been built and the eggs are incubating, the birds may continue to add material to the nest (Warham 1990). The nest building time is an important bonding time

between breeding pairs (Nelson 1980). In species that collect and use nest material, it is often the male that brings most of the material, and the female who builds the nest (Nelson 1980). The masked booby makes several hundred trips on foot to bring material to build the nest (Nelson 1980). Frigates steal the majority of their nest material from other frigates and boobies (Nelson 1980). In some species, when the breeding pair switch incubating, the female may bring nest material to patch up the nest (Nelson 1980). Burrows a made by excavating the dirt with the beak and feet and then it is kicked out behind the bird (Nelson 1980). Burrow nests are often lined with leaves, moss and twigs which are carried in from the outside the burrow (Furness 1987). Albatross species take raw material from around the nest site and make a hallow in the middle (Nelson 1980). The African gannet retains its excretion matter while at sea and deposits guano as nest material (Nelson 1980). Storm petrels rim their nests with frozen stomach oil and guano (Warham 1990). Breeding performance is greatly influence by nest site quality (Furness 1987), the birds in higher quality nests have greater reproductive success.

- Nest Site Fidelity

Breeding site and nest site fidelity is common in seabirds. Birds will often select the site used by their parents, or a similar one (King 1983). Male gannets are faithful to their sites and mates 94% of the time (Nelson 1980). When site fidelity is present in a species, the birds are often faithful to their mates as well. Site fidelity particularly occurs when the birds have built or dug elaborate nests and burrows. This behaviour has evolved because of the high cost of establishing a new nest site (Lofgren 1984).

Nest site fidelity has many benefits and costs to seabirds (Table 2).The cost of nest site fidelity is that the birds may return to a low quality site year after year which may reduce their environmental success (Bried 2002). If they loose their mate between the breeding seasons, the birds may wait for a lost mate that will never return, and so loose all hope of breeding that season. The benefits of nest site fidelity is increased breeding success as they do not need to search for nests or build new nests, and so reproductive performance is increased (Bried 2002). The birds know the resources of an area better as they become familiar with the site, so they can find food and shelter more effectively. Because of the increased knowledge of the resources, they often have more success in contests for territories.

Nest site fidelity is proportional to the effort involved in maintaining the site, it is common in burrowing birds because a lot of trauma and effort is involved in digging a new burrow (Nelson 1980). The waved albatross make no nest and do not remain faithful to their nesting sites (Nelson 1980).

Table 2: Costs and Benefits of Site Fidelity Source (Bried 2002)

Benefits	Costs
Increased breeding success	Low breeding success when remaining on a low quality site
Better knowledge of neighbours and potential mates	Failure to breed when remaining on the territory after loss of mate
Dominance in territorial contests	Costs of territorial defence
Utilisation of the site as a meeting point for pairs to reunite hence all the benefits from mate retention	

EGG LAYING

- General egg laying patterns

The pre-laying and laying patterns in sea birds vary within species and orders. Copulation tends to take place onshore in all species of seabirds, but the fertilization of the ovum generally occurs at sea (Whittow 2002). The length that birds spend at sea feeding after mating and before laying varies between species, it depends on body size and the migratory status of the species (Warham 1990). In the Great Albatross it is 7% of the reproductive cycle, and in the shearwaters, storm petrels and prions it is 30-38% of the reproductive cycle (Warham 1990). The pre-laying period (after fertilisation but before laying) is relatively short in most seabird species, but can be long in birds in that breed in temperate latitudes (Lofgren 1984). For Adelie penguins, yolk deposition begins at sea and takes between 14 and 17 days (Astheimer 1985). Egg formation in petrels is similar in process but takes longer than most seabirds. It is the period of yolk deposition that takes longer, not the laying (Warham 1990).

The laying period in a colony is spread over a few days, the first time breeders tend to arrive at the colonies first but lay later than experienced breeders (Warham 1990). Female's generally lay one egg every two days until clutch size is complete and incubation can begin, if an egg is lost before the clutch is complete, then females may continue to lay every two days until it is complete. During egg laying, the Layson albatross stands with its cloaca contracting and dilating for nine minutes, the egg is then dropped, inspected and then it settles upon the egg for incubation (Warham 1990). Laying occurs both during the night and during the day, depending on the species. Many

burrowing petrels tend to lay at night, but the Laysons and Wandering Albatross' tend to lay during the day (Warham 1990).

Coloniality can affect the timing of egg laying and female investment in the eggs (Davis 2003), females in the colony may synchronise their breeding so that the eggs are all laid at the same time, this generally happens in most bird colonies. Synchrony of breeding in colonies does not appear to be higher in seabirds than the other bird types. Just like in the other bird types, synchrony of breeding does not always occur, for example the European Shags in a colony may lay their eggs over a period of many weeks (Coulson 2002).

Most eggs are oval in shape, and they are more pointed at one end than the other. They are oval in shape because they have been pushed out the oviduct during laying. Cliff-nesting birds often have conical shaped eggs. This occurs to reduce the likely hood of the eggs rolling off the cliff. Hole-nesting birds have spherical eggs as they are in no risk of rolling off a cliff. Colours and markers are on the eggs for individual recognition and camouflage, this is important when the birds nest close together or have no nest (Nelson 1980). Hole nesters usually have white eggs (Nelson 1980).

- <u>Size difference between eggs</u>

The general trend in seabirds is a clutch size of two eggs. The second is usually the smaller of the two eggs and the laying interval between the two is 1-2 days, but in some penguin species it can be up to four days (Hamer 2002). In Rockhopper and Macaroni penguins, the first egg of the two is smaller and it usually dries up after hatching. It is most often the second egg that hatches and that chick is raised (King 1983). (Nelson 1980) found that in Macaroni penguins, the second egg is on average 71% heavier than

the first. In crested penguins it is the first laid egg that is generally larger but it is the second egg that hatches first. This is because it is incubated at the posterior region of the adult body which is warmer (Burger 1979).

Yellow-Eyed penguins lay two eggs, they both hatch and the parent usually raises both (Nelson 1980). In Masked boobies, the second chick is a safety net (if the first chick dies) and is usually rejected and often killed by the first chick (Nelson 1980). In petrels and albatrosses, eggs from the same female tend to be similar in size (Brooke 2004).

- Clutch size

Seabirds lay relatively few eggs compared to the other bird types. In general, seabirds lay clutches of one or two eggs with 54% of seabird species lay clutches consisting of only a single egg (Hamer 2002). An unusual example is some skimmer species, which lay up to seven eggs in one clutch. It is hypothesised that seabirds lay small clutches because food resources are scarcer in the marine environment that in terrestrial environments (Hamer 2002). This means the food resources are able to support fewer birds and so the selection pressures upon the birds are to lay fewer eggs and invest more parental effort into raising the chicks. This ensures that when they are older, they can compete with the other adult birds for food resources. This is why seabirds are generally k-selected species with high parental care and high adult survival (Furness 1987). It is the high cost of raising a chick that probably results in the evolution of single egg clutches in seabirds, not the cost of egg production (Hipfner 2003).

Most Auks and Gannets only lay one egg and they are unable to replace it, if it is lost. All birds in the order *Procellariiformes* (Albatrosses, fulmars, shearwaters ad petrels) lay one

egg (Dunnet 1990). King and Emperor Penguins also lay a single egg, but most of the smaller penguin species lay two eggs (King 1983). One egg clutches are normal in petrels, but clutches of more than one do occur, they often occur because of the intervention of another female who lays an egg in the nest when the nest occupier is away feeding (Warham 1990).

Egg clutches are smaller in off shore feeders such as birds in the order *Procellariiformes* and tropical seabirds which are largest in the cormorants and terns (Whittow 2002). Birds that nest far from food resources lay smaller clutches because food is the primary limitation to clutch size (Nelson 1980). More eggs in a clutch put more strains on the food resources, so if food resources are closer, then more eggs can be raised, this is why clutch size is larger in near shore feeders than pelagic feeders (Hamer 2002). In general, heavier females produce larger clutch sizes (Chastel 1995).

- Factors that influence egg development and laying

Young and inexperienced females often face problems when breeding. These occur in delayed laying, reductions in egg mass and proportional yolk content. The biochemical composition of eggs does not change with experience or age. (Hipfner 2003) studied egg laying behaviour in thick-billed murres (*Uria Lomvia*) and found that the young and inexperienced females laid eggs 4-18 days later than the population mean. Their eggs also averaged 13% lighter in mass and had lower yolk to albumen ratios.

Some seabird species lay a replacement egg when one of their eggs is lost. Predation and bad weather conditions are the main two reasons eggs are lost. It is often the older, more experienced females, and those females in better condition that relay (Hipfner 2003). The

chicks that hatch from replacement eggs often have higher rates of mortality. (Hipfner 2003) found that replacement eggs in thick-billed murres were on average 6% lighter than first eggs and had a lower yolk-albumen ratio. Relaying after an egg is lost is rare in petrels (Warham 1990). Adelie penguins generally lay clutches of two eggs, and 65% of females will lay a third egg if their first is lost in the first 24 hours, and some may lay a fourth (Taylor 1962). A reason offspring from replacement clutches often have lower survival rates than those that hatch in the first clutch is possibly because the fledglings hatch late and are socially subordinate, and also the food supplies have been exhausted (Hipfner 1997). An exception is thick-billed murres, chicks from replacement eggs are just as likely to survive, they have the same survival rate as those chicks that hatch from the original clutch (Hipfner 2001).

The condition a penguin is in will determine when and whether it will breed (Davis 2003). If a bird is in a bad condition health wise, it may not be able to attract a mate, or may not be in a state to lay a fertile egg. Female birds that lay more than the normal number of eggs for their species may be more prone to disease (Oppliger 1996).

In male blue petrels, body condition is positively related to breeding experience, and breeding experience influences a male's decision to breed. Female blue petrel breeding performance is related to breeding experience but not body condition. While breeding performance is not related to body condition, egg formation is (Chastel 1995).

In many seabird species, egg and clutch size increases with increasing female age, and declines with laying date (Hipfner 1997). This is possibly because young birds initiate egg formation later. (Hipfner 1997) studied Thick-billed Murres and found that egg size

declined with laying age among young females, and that egg size was independent of laying date among older birds.

(Verboven 2005) studied lesser black-backed gull (Larus fuscus) and found that intra-specific interactions experienced by female birds during their egg formation can influence the conditions for embryonic development.

- Egg size in relation to female body size

Seabirds are large birds so they lay larger eggs, but egg size varies greatly between species (Whittow 2002). Seabird eggs range in size from 5.5 grams in the Storm Petrel to 638 grams in the Emperor Penguin (Whittow 2002). The petrels and albatross species lay large, heavy eggs in relation to their body size (Warham 1990). The largest eggs are laid by the bird species that breed furthest away from the sea and food sources, and those that raise downy young (Nelson 1980). The British and black bellied storm petrels in the *Procellariiformes* order lays eggs that are 26% of the females weight, this is the largest egg size in relation to female body size (Nelson 1980). The smallest eggs in relation to female body size are the penguins and pelicans (Nelson 1980).

- Egg composition

A bird's egg is made of egg white and yolk. The larger end of the egg contains an air cell that forms when the content of the egg has cooled and contracted, after it is laid. The yolk of an egg is a food source for the developing embryo and it is suspended in the egg white of the egg. This usually makes up 33% of the liquid weight of an egg. Species with downy yolk have more yolk in their eggs compared to those whose young hatch naked

(Nelson 1980). Egg white is also called albumen, and its purpose is to protect the egg yolk. It also provides additional nutrients for the embryos growth and is 83% water. Yolk and albumen production and quantities may vary between species, with the yolk generally comprising between 14.2% and 46.6% of the egg contents (Whittow 2002). The differences in egg yolk contents between species are related to variation in hatching maturity (Whittow 2002). In Adelie penguins, egg mass decreases with laying order, but the ratio of albumin to yolk mass stays the same (Astheimer 1985).

Birds eggs are surrounded by a thin hard shell, in petrels the shell is about twice as dense as the egg contents (Warham 1990). The shell of a usually makes up 10-12% of the weight of a fresh egg. Gannets have exceptionally thick shells because they are heavy birds that incubate the eggs under their feet (Nelson 1980), so the shell must be able to support the weight of the bird. Larger eggs tend to have relatively larger shells (Brooke 2004).

Table 3: Composition of Seabird Eggs Source:(Whittow 2002)

Seabird Type	Egg Mass (g)	Shell (% of egg mass)	Yolk (% of egg contents)	Water (% of egg contents)
Sphenisciformes	166.2	13.5	28.4	78.5
Procellariiformes	147.5	8.5	37	75.9
Pelecaniformes	69.7	11.8	21.7	81.9
Charadriiformes	54.2	7.9	32.8	75.5

CONCLUSION

Seabirds are birds that feed on marine food resources. They are dependent on land for space to breed and all seabird breeding occurs on land. Seabirds are found in all the oceans throughout the world, in both hemispheres. Seabirds generally breed in colonies of varying size, these colonies are often found on the cliffs of offshore islands. Within these colonies they nest in burrows, trees, crevices and some species build no nests. Nest sites are chosen in areas that provide protection for the birds from potential predators, weather, and human disturbance.

Food resources are also important in deciding where to nest as they must be able to support the adults and their chicks. Nest territories are set up by the birds upon arrival to the colony and in most species it is the males who defend the nest territory and collect the material to build the nests. Nest site fidelity is high in seabirds, and many species return to the nest site they were born at.

Fertilisation of eggs takes place on land, and then the birds often return to sea for a period before laying to feed. The pre-laying period is relatively short in seabirds compared to other bird types. Seabirds generally lay two eggs, and the second is often smaller than the first. Clutch size is two because food resources are scarcer in the marine environment than terrestrial environments, so there are more selection pressures to raise fewer and larger young. They are usually white and oval in shape. Many seabird species are able to replace an egg if it is lost before hatching. These relayed eggs often have lower hatching and survival rates. Seabirds lay eggs that are relatively large in relation to the female's body size. Female age and experience, weather, and the adult's body condition are all factors that influence egg laying and breeding behaviour.

This report has looked at the different aspects of seabird nest site selection and egg laying behaviour, general characteristics have been established and summarised. Many of the characteristics have been explained using evolutionary aspects. The knowledge this project has provided on seabird breeding behaviour is phenomenal and great experience has been gained in researching and writing the report on this topic.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr Melanie Massaro from Biological Sciences at the University of Canterbury for providing help and guidance with this project.

I would like to thank the staff at Gateway Antarctica for their help and support in finding a suitable project topic, and also their continued support throughout the Graduate Certificate in Antarctic Studies course work.

REFERENCES

Astheimer, L., Grau, CR (1985). "The timing and energetic consequences of egg formation in the Adelie penguin." The Condor **87**: 256-268.

Bried, J., Jouventin, P (2002). Chapter 9: Site and Mate Choice in Seabirds: An evolutionary approach. Biology of Marine Birds. J. B. EA Schreiber. USA, CRC Press LLC**:** 263-305.

Brooke, M. (2004). Albatrosses and Petrels across the world. New York, Oxford University Press.

Burger, E., Williams, AJ (1979). "Egg temperatures of the Rockhopper penguin and some other penguins." Auk **16**: 100-105.

Chastel, O., Weimerskirch, H, P Jouventin (1995). "Influence of body condition on reproductive success in the blue petrel." Auk **112**(4): 964-972.

Clode, D. (1993). "Colonially Breeding Seabirds: Predators of Prey?" Trends in Ecology and Evolution **8**(9): 336-338.

Coulson, J. (2002). Chapter 4: Colonial Breeding in Seabirds. Biology of Marine Birds E. S. a. J. Burger. USA, CRC Press LLC**:** 87-113.

Cramp, S. (1985). Birds of the Western Palearctic. Oxford, Oxford University Press.

Davis, L., Renner, M (2003). Penguins. London, T&AD Poyser.

Dunnet, G., Furness RW, Tasker, ML, Becker, PH (1990). "Seabird Ecology in the North Sea." Netherlands Journal of Sea Research **26**(2-4): 387-425.

Furness, R., Monaghan, P (1987). Seabird Ecology. New York, USA, Chapman and Hall.

Hamer, K., Schreiber, EA, Burger, J (2002). Chapter 8: Breeding Biology, Life Histories, and Life History - Environment Interactions in Seabirds. Biology of Marine Birds. E. S. a. J. Burger. USA, CRC Press LLC**:** 217-261.

Hipfner, J., Gaston AJ, deForest LN (1997). "The role of female age in determining egg size and laying date of thick-billed Murres " Journal of Avian Biology **28**(4): 271-278.

Hipfner, J., Gatson, AJ, Herzberg, GR, Brosnan, JT, Storey, EA (2003). "Egg composition in relation to female age and relaying: Constrants on egg production in thick-billed murres (*Uria Lomvia*)." Auk **120**(3): 645-657.

Hipfner, M. (2001). "Fitness-related consequences of relaying in an Arctic seabird: Survival of offspring to recruitment age." Auk **118**(4): 1076-1080.

King, W. B. (1983). "Seabird Breeding Habits." Oceanus **26**(1): 28-35.

Lack, D. (1966). Proccedings XIV International Ornithological Cong. New Zealand Ornithological Trust Board**:** 3-42.

Lofgren, L. (1984). Ocean Birds: Their breeding, biology and behaviour. Sweden, Croom Helm Ltd.

Nelson, B. (1980). Seabirds: Their biology and ecology. England, The hamlyn publishing group limited.

Oppliger, A., Christe, P, Richner, H (1996). "Clutch size and Malaria resistance." Nature **381**: 565.

Schreiber, E., Schreiber, RN, Schenk, GA, Ed. (1996). Red-Footed Booby. Birds of North America. Washington DC, Academy of Natural Sciences, Philadelphia: American Ornitholoists Union.

Taylor, R. (1962). "The Adelie Penguin *Pygoscelis adeliae* at Cape Royds." Ibis **104**: 176-204.

Verboven, N., Evans, NPB, D'Alba, LA, Nager, RGA, Blount, JDA, Surai, PFC, Monaghan, PA (2005). "Intra-specific interactions influence egg composition in the lesser black-backed gull (Larus fuscus)." Behvaioural Ecology and Sociobiology **57**(4): 357-365.

Warham, J. (1990). The Petrels: Their Ecology and Breeding Systems. London, Academic Press.

Whittow, G. (2002). Chapter 12: Seabird Reproduction Physiology and Energetics. Biology of Marine Birds. J. B. EA Schreiber. USA**:** 409-437.